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Geographic Variation in *Bufo valliceps* (Anura: Bufonidae), a Widespread Toad in the United States and Middle America

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ABSTRACT The common lowland toad *Bufo valliceps* has a large distribution in the southern United States, Mexico, and most of Central America; this ample distribution across diverse temperate and tropical habitats is unusual among frogs. Geographic variation in size, shape, skin texture, and color pattern among populations of this species was reviewed. Although there are great differences between extreme northern and southern popula-

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tions, I did not find smooth clinal variation for any character examined. Nor is there a discrete break among these continuous morphological variables that separate the the northern and southern morphs. Variation in *Bufo valliceps* is characterized by a high degree of inter- and intrapopulational variation that cannot be attributed to simple trends associated with latitude, elevation, or climate. An analysis the relationship between body size and aridity, along a precipitation gradient on the Yucatan Peninsula, found no consistent covariation. Previous claims for a postive relationship between elevation and degree of development of the cranial crests were found not to be accurate. Although the several relatively distinct populations are referable to the taxa *Bufo nebulifer* and *Bufo valliceps wilsoni*, I do not propose recognition of these taxa, pending further research.

Key words: Bufonidae; *Bufo valliceps*; Geographic variation; Middle America; Systematics.

INTRODUCTION

Bufo valliceps is a ubiquitous species that occurs in open habitats from extreme southwestern Mississippi, across Texas to the Big Bend region, southward along the Atlantic coast to extreme northeastern Costa Rica, and across the Isthmus of Tehuantepec and southeastward along the Pacific coasts of Chiapas and Guatemala, at elevations from sea level to 1700 m (Fig. 1). This distribution includes an enormous variety of habitats and climatic regimes—e.g., relatively aseasonal rainforests of eastern Nicaragua; dry and seasonally cold Chihuahuan desert of Val Verde County, Texas; wet and seasonally cool swamps of southern Louisiana; cool and perpetually wet Atlantic slopes of the Chiapas highlands in Mexico; and hot and seasonally dry thorn forest in the upper Grijalva River Basin of Huehuetenango, Guatemala. However, *B. valliceps* seems to be ubiquitous in open habitats, whether the grasslands are natural (e.g., the Texas Gulf Coast) or the secondary growth and pastures resulting from human activities in areas of former rainforest in eastern Guatemala (Mendelson, 1994). The habitat preference of *B. valliceps* resembles that of the well-known human commensal *Bufo marinus* (Zug and Zug, 1979) in that the toad is often abundant in villages and agricultural areas.

Porter (1962, 1963, 1964, 1970) reviewed the taxonomic status, distribution, and geographic variation of *Bufo valliceps*, with special reference to Mexican populations. He acknowledged a great amount of morphological variation across its geographic range, especially with respect to overall size, skin texture, and development of cranial crests. Nevertheless, Porter (1970) chose not to recognize any of the subspecies that had been proposed—viz., *B. valliceps macrocristatus* Firschein and Smith from the Atlantic rainforests of Oaxaca; *B. valliceps wilsoni* Baylor and Stuart from the Grijalva Valley of Chiapas and adjacent Guatemala; and *B. valliceps microtis* Werner from Honduras. Subsequent to Porter's papers, more specimens from remote regions of southern Mexico have been collected; these specimens allowed for resolution of taxonomic problems pertaining to certain populations that were referred by Porter and others variously as *B. cavifrons*, *B. cristatus*, and *B. valliceps*. Mendelson (1994, 1997a,b) reviewed much of this newer material and recognized or described *B.*

macrocristatus, *B. campbelli*, *B. spiculatus*, *B. tutelarius*, all of which had previously been confused, at least partially, with *B. valliceps*. Mendelson (1998) referred the taxon *B. valliceps microtis* to the synonymy of *B. coccifer*. Although it is clear that some of the morphological variation observed by Porter is attributable to species-level variation that occurs among these newly recognized species, the fact remains that *B. valliceps* has a large geographic distribution and exhibits remarkable morphological variation.

In the northern areas of its range, *B. valliceps* are larger than are conspecifics in southern Mexico and Central America (Porter, 1970). Blair (1963, 1972) commented generally on differences in dorsal color, throat color in males, and size among populations from northern and southern extremes of the range. Porter (1964) summarized geographic variation in snout-vent length (SVL) and characteristics of the advertisement calls of males for populations from Texas through southern Mexico, and Porter (1962) summarized other morphological variation in these same populations. The remarkable level of variation in color patterns among individuals of *B. valliceps* from Nicaragua and the Yucatan Peninsula were discussed by Villa (1972) and Lee (1993), respectively. Finally, several authors (Porter, 1963, 1964; Blair, 1966, 1972; Branson, 1995) have reported that the height of the cranial crests is directly correlated with the elevation at which a particular population occurs; this claim warrants specific attention and is discussed in more detail.

Herein, I summarize geographic variation in *Bufo valliceps*, and replicate part of Lee's (1993) analysis of variation in anuran body size along the precipitation gradient on the Yucatan Peninsula. I also address other apparent trends in morphological variation among populations of *B. valliceps*, and I discuss the remaining taxonomic issues of the status of *B. valliceps wilsoni* and *Bufo nebulifer* Girard. This study is a complement to those of K. R. Porter (1962, 1963, 1964, 1970), but differs by considering the entire range of the species, excluding several populations that are now known to represent different species (Mendelson, 1997b, 1998), and by being based on more specimens than were available to Porter.

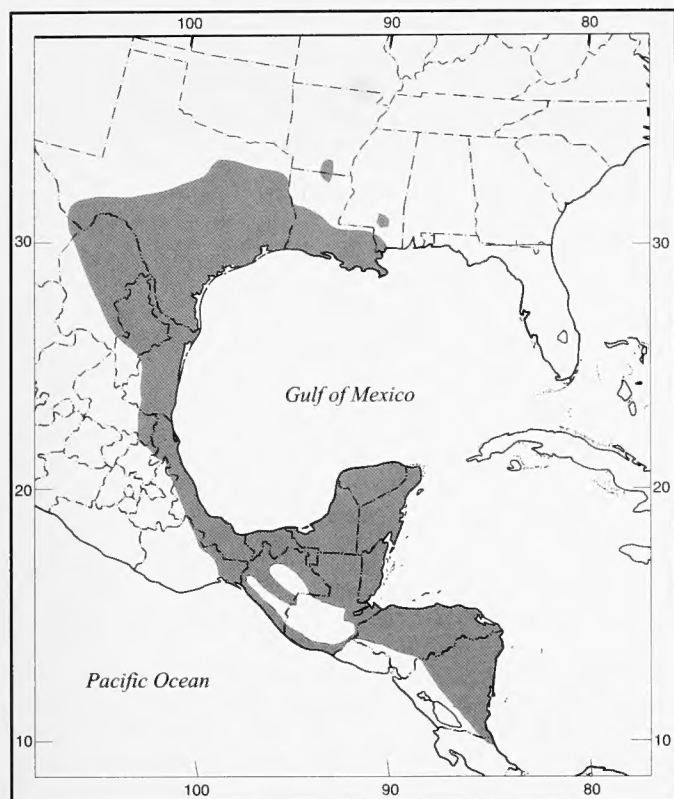


Fig. 1. Geographic distribution of *Bufo valliceps*, modified from Porter (1970) and excluding erroneous records from El Salvador and western Nicaragua (Frost, 1985:52, 63). *Bufo valliceps* is absent in all areas above 1700 m of elevation.

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Fig. 2. Map showing the location of the 19 samples of *Bufo valliceps* studied in the range-wide morphometric analyses: (1) Baton Rouge, East Baton Rouge Parish, Louisiana; (2) Walker County, Texas; (3) Tarrant and Dallas counties, Texas; (4) Austin, Travis County, Texas; (5) Liverpool, Brazoria County, Texas; (6) Brownsville, Cameron County, Texas; (7) Val Verde County, Texas; (8) Don Martin Dam, Coahuila; (9) Huejutla, Hidalgo; (10) Cuautlapam, Veracruz; (11) Acayucan, Veracruz; (12) Tuxtla Gutierrez, Chiapas; (13) Chinajá, Alta Verapaz, Guatemala; (14) Escárcega, Campeche; (15) Pueblo Nuevo X-Cán, Quintana Roo; (16) Tucuru, Alta Verapaz, Guatemala; (17) Champerico, Retalhuleu, Guatemala; (18) San Pedro Sula, Cortés, Honduras; (19) Condega, Estelí, Nicaragua. Inset shows the mean snout-vent length and 95% confidence intervals for populations. Sample sizes for each population are shown in Table 4.

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MATERIALS AND METHODS

I examined specimens of *Bufo valliceps* from all areas of its range between Louisiana and Estelí, Nicaragua; I have not seen specimens from Mississippi, Arkansas, or Costa Rica, but rely on reports by others (Conant and Collins, 1991; J. M. Savage, pers. comm.) for the accuracy of these records. Note that for localities from the USA or Mexico only state or county designations are provided. The mor-

phometric survey included only adult males from 19 populations (Fig. 2); sexual maturity was assessed by presence of nuptial excrescences and vocal slits. The following morphometric features were measured in a manner following that of Duellman (1970:fig. 2): snout-vent length (SVL); tibia length (TIB); foot length (FTL); head length (HL); head width (HW); tympanum width (TYMP). The following

Table 1. Results of the first four principal components explaining 89% of the variation in a PCA (covariance matrix) performed on 15 log-transformed morphometric variables measured on male *Bufo valliceps* representing 19 populations from throughout the range of the species. Loadings of each variable are also shown.

Variable	PC 1	PC 2	PC 3	PC 4
Eigenvector	0.057243	0.003921	0.002469	0.001992
Proportion of variance	0.780	0.053	0.034	0.027
Cumulative proportion	0.780	0.833	0.867	0.894
SVL	-0.258	0.023	0.078	0.113
FML	-0.292	-0.066	0.248	0.042
ML	-0.252	0.081	0.058	-0.074
RUL	-0.234	0.134	0.177	-0.016
HDL	-0.246	0.032	0.102	-0.042
TIB	-0.252	0.102	0.389	-0.569
FTL	-0.246	0.017	0.147	-0.128
HL	-0.258	0.026	0.120	0.072
HW	-0.284	0.089	0.106	0.055
ORB	-0.188	0.041	0.091	0.088
END	-0.234	0.085	-0.122	0.462
TYMP	-0.263	-0.135	0.083	0.577
SPTYMP	-0.270	0.660	-0.608	-0.109
PARL	-0.308	-0.418	0.460	-0.279
PARW	-0.267	-0.560	-0.277	-0.091

features were measured in a manner following that of Mendelson (1994): orbit diameter (ORB); eye-nostril distance (END); length of supratympanic crest (SPTYMP); length of parotoid gland (PARL); width of parotoid gland (PARL). The following features were measured in a manner following that of Lee and Crump (1981): femur length (FML); metatarsal length (ML); radioulna length (RUL);

hand length (HDL). All measurements were taken with digital calipers, rounded to the nearest 0.1 mm, and log-transformed. Principal components analysis (PCA; covariance matrix), One-Way ANOVA, and Tukey's Method for Unplanned Comparisons were performed using MINITAB (Macintosh ver. 10.5; Minitab Statistical Software, 1995). Stepwise discriminant function analysis (DFA) was performed using the BMDP computer program.

RESULTS

GEOGRAPHIC VARIATION IN SIZE

Bufo valliceps from the northern part of the range are substantially larger than most individuals of the species from southern Mexico and Central America. Differences in mean SVL among the 19 populations are shown in Figure 2; ANOVA indicated significant differences among these populations ($F = 42.29$; $df = 18$; $P < 0.0001$).

Range-wide comparisons.—The loadings resulting from a PCA of the 15 morphometric variables measured on adult males representing these 19 populations are displayed in Table 1. The first four principal components (PC) accounted for 89.4% of the variation. All of the loadings on the first PC were of the same sign and of similar magnitude and, therefore, seem to represent overall size and size-correlated variation among all variables. The remaining PCs represented nonsize-correlated variation within the sample. The PC II has a strong positive loading for SPTYMP and high negative loadings for PARL and PARW. The PC III also had similar high loadings for SPTYMP (negative loading) and PARL (positive loading), as well as relatively high negative loadings for PARW, FML, and TIB. The PC IV had a high negative loading for TIB and high positive loadings for END, and TYMP. Despite these strong loadings, plots of individual scores on PC I–IV showed little dispersion among the representatives of the populations; PC II–

IV explain relatively little variation. Therefore, I directed my efforts toward comparison of overall size using PC I as an indicator.

An ANOVA of scores on PC I revealed significant differences in overall size among the 19 populations between Texas and Estelí, Nicaragua ($F = 37.95$; $df = 18$; $P < 0.0001$). Tukey's Method identified homogenous sets of these populations based on overall size (Fig. 3) and demonstrated a general trend of size-increase with increased latitude. However, this trend is not entirely consistent. For example, the sample from Brazoria County, on the Gulf Coast of Texas, is contained within sets that include samples from Guatemala and Nicaragua; likewise, the sample from Louisiana is contained within sets including populations from southern Mexico and Guatemala. The largest toads in this analysis form a small set of two samples from central and western Texas. The sets containing the next overall largest toads included samples from most of the northern populations (excluding Louisiana and Brazoria County, Texas), as well as samples from Huejutla, Hidalgo (south of the Tropic of Cancer) and from Pueblo Nuevo X-Cán, Quintana Roo, at the northeastern tip of the Yucatan Peninsula. A mid-sized group of sets includes a variety of disjunct localities including Louisiana, southern Texas, Cuautlapam (Veracruz), and two samples from near the base of the Yucatan Penin-

Table 2. Results of the first four principal components explaining 81% of the variation in a PCA (covariance matrix) performed on 15 log-transformed morphometric variables measured on male *Bufo valliceps* representing nine populations from across the length of the Yucatan Peninsula. Loadings of each variable are also shown.

Variable	PC 1	PC 2	PC 3	PC 4
Eigenvector	0.017310	0.003854	0.002758	0.002265
Proportion of variance	0.537	0.120	0.086	0.070
Cumulative proportion	0.537	0.657	0.742	0.813
SVL	-0.237	-0.089	0.017	0.034
FML	-0.308	0.931	0.151	0.053
ML	-0.247	-0.048	-0.010	-0.070
RUL	-0.215	-0.095	-0.025	0.071
HDL	-0.257	-0.118	0.027	0.110
TIB	-0.182	-0.079	0.006	0.025
FTL	-0.193	-0.146	-0.014	0.010
HL	-0.235	-0.122	0.099	-0.071
HW	-0.300	-0.121	-0.083	0.756
ORB	-0.317	0.043	-0.767	-0.435
END	-0.315	-0.171	0.608	-0.451
TYMP	-0.261	-0.079	0.017	0.003
SPTYMP	-0.276	-0.050	0.004	0.059
PARL	-0.243	-0.043	-0.007	0.012
PARW	-0.239	-0.040	0.007	-0.031

sula. The sets containing the smallest toads included samples from northern (Brazoria County, Texas), intermediate (Acayucan, Veracruz, and the Grijalva Valley of Chiapas and adjacent Guatemala), and southern localities (Nicaragua and the Pacific Coast of Guatemala). These results suggest that in the northern area of their range, *B. valliceps* are larger than those in the southern areas, but there is no smooth north-south cline in overall size.

These results provide conflicting evidence with respect to the hypothesis that anurans from more xeric environments are larger than those from more mesic areas. For example, the largest toads are from areas that receive little mean annual rainfall: 855 mm (Dallas, Texas; 1961–1990), 810 mm (Austin, Travis County, Texas; 1961–1990), and 472 mm (Del Rio, Val Verde County, Texas; 1961–1990); a female (UTA A-7228) collected by J. A. Campbell near Fort Worth, Texas, has an SVL = 121.3 mm. However, toads from areas receiving similarly scant amounts of rainfall were much smaller (Figs. 2, 3)—e.g., for example: 675 mm, Brownsville, southern Texas; 832 mm, Cintalapa, Chiapas (= Grijalva Valley; rainfall data from Johnson, 1990). The smallest toads did come from rather wet areas: 1220 mm (San Pedro Sula, Depto. Cortes, Honduras; 1944–1982); 2500 mm (Tapachula, Chiapas, [near Champerico, Guatemala]; Shelford, 1963); and 1740 mm (Veracruz, Veracruz [near Acayucan]; 1971–1980). However, Chinajá, Alta Verapaz, Guatemala, receives about 4000 mm of rain each year (Duellman, 1963), and the sample of toads from this locality was not among the smallest in this study (Figs. 2, 3).

Size variation along a precipitation gradient.—The loadings resulting from PCA of the 15 morphometric variables from nine populations over the length of the Yucatan Pen-

insula are displayed in Table 2. The first four PCs accounted for 81.3% of the variation among the specimens included in the analysis. As with the overall analysis, all of the loadings on PC I are of the same sign and of similar magnitude and, therefore, seem to represent overall size and size-correlated variation among all variables. The remaining PCs represent nonsize-correlated variation within the sample. The second PC has a high positive loading for FML, PC III has high negative loadings for ORB and END, and PC IV has a high positive loading for HW. Despite these strong loadings, plots of individual scores on PC I–IV showed little dispersion among the representatives of the nine populations. However, there are significant differences in overall size among the samples of *B. valliceps*, as indicated by the results of an ANOVA on PC1 scores ($F = 6.07$; $df = 8$; $P < 0.0001$). The mean score for PC I and standard deviation for each population, and the homogeneous subsets of populations identified by Tukey's Method are shown in Figure 4. Toads from the more xeric northwestern portion of the peninsula (e.g., Mérida, Chichén Itzá) are not significantly larger than those from the rainforests of Chinajá, Guatemala (Fig. 4). In fact, the two populations that compose a distinct subset in this analysis are from opposite ends of the peninsula—La Libertad, El Petén, Guatemala, and Pueblo Nuevo X-Cán, Quintana Roo. La Libertad lies in a savanna habitat having a relatively high, but seasonal, rainfall, whereas Pueblo Nuevo X-Cán lies in a region that has unusually high rainfall compared to the rest of the northern peninsula (Lee, 1980).

Discriminant Function Analysis.—In order to identify which morphometric measurements most effected separation among groups and to determine degree of

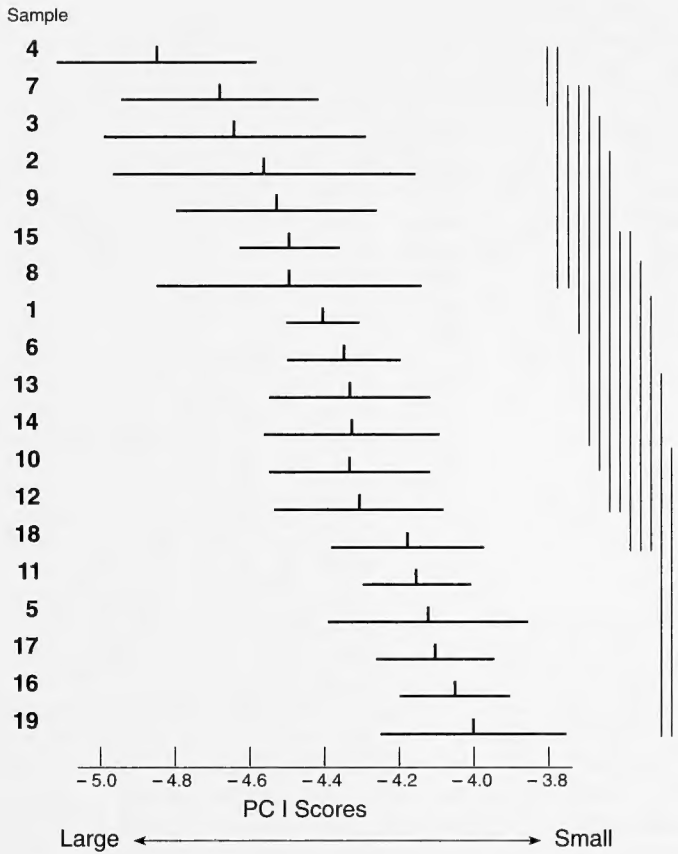


Fig. 3. Mean scores with 95% confidence intervals on Principal Component I for each sample population of *Bufo valliceps* (Fig. 2), ranked by magnitude. The vertical bars to the right indicate homogeneous subsets of samples identified by Tukey's Method. Sample sizes for each population are shown in Table 4.

morphomeric distinctiveness among samples, I performed an initial stepwise DFA of the 15 morphometric variables from the 19 sample populations of (Fig. 2). All variables except TIB varied significantly among groups ($F < 0.05$) in the initial analysis; a second analysis that specified the 14-variable model for the canonical discriminant analysis was performed. Group means were different ($F < 0.001$) at each step in the 14-variable model and 100 % of the variation was displayed on five canonical axes; the first two axes displayed 99 % of the variation (CAN I, CAN II; Fig. 5). Review of the standardized (pooled within-group variances) coefficients for the canonical variables (Table 3) reveals that dispersion on CAN I is primarily because of variance among groups in the following variables: snout-vent length; foot length; head width; orbit diameter; and eye-nostril distance. Dispersion on CAN II also was caused by variance in snout-vent length, foot length, and head width, but this axis also displayed dispersion caused by variance among groups in head length and parotoid width.

None of the 19 sample populations had 100 % correct classifications in the jackknifed classification matrix of the

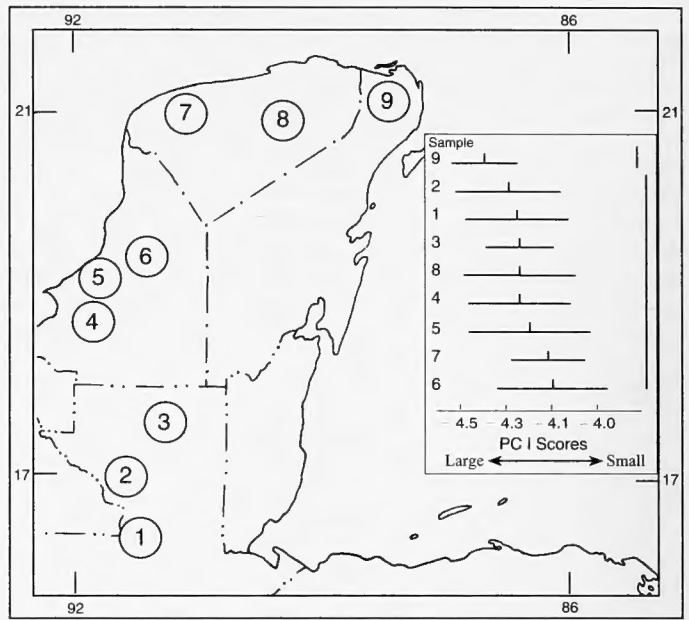


Fig. 4. Map of the Yucatan Peninsula showing location of nine samples of *Bufo valliceps* used in the morphometric analysis along the Yucatán precipitation gradient [sample sizes in brackets]: (1) Chinajá, Alta Verapaz, Guatemala [19]; (2) La Libertad, El Petén, Guatemala [4]; (3) Tikal, El Petén, Guatemala [9]; (4) Escárcega, Campeche [19]; (5) Champotón, Campeche [7]; (6) Dzibilchen, Campeche [4]; (7) Mérida, Yucatán [6]; (8) Chichen Itzá, Yucatán [10]; (9) Pueblo Nuevo X-Cán, Quintana Roo [12]. Inset shows mean scores and 95% confidence intervals for each sample on Principal Component I, ranked by magnitude. The vertical bars to the right indicate homogeneous subsets of samples identified by Tukey's Method.

14-variable model (Table 4). The samples with the highest percentage of correct classifications were Sample 11 (92.3%), Sample 5 (91.7%), Sample 1 (87.5%), and Sample 12 (82.1%). The samples with the lowest percentage of correct classifications were Sample 2 (13.3%); Samples 7 and 8 (25.0%), and Sample 3 (35.7%). The pattern of misclassifications (Table 4) indicates a slight geographic trend among the samples. Northern toads (Samples 1–8) tended to be misclassified as members of other northern samples. Toads from more southerly samples (Samples 6, 9) were primarily misclassified as members of either more northern or more southern samples, and southern toads (Samples 10–19) tended to be misclassified usually as members of other southern populations, but also as members of any but the largest northern samples (Samples 3, 4, 7, 8).

QUALITATIVE COMPARISONS

There is considerable variation in external features of *Bufo valliceps*. As with the morphometric variation described above, there are some geographic trends, but inter-individual variation in dorsal pattern and skin texture obfuscate discrete characterizations of the different populations.

Toads from northern localities (e.g., USA, northern Mexico) are remarkably consistent in having a sharply

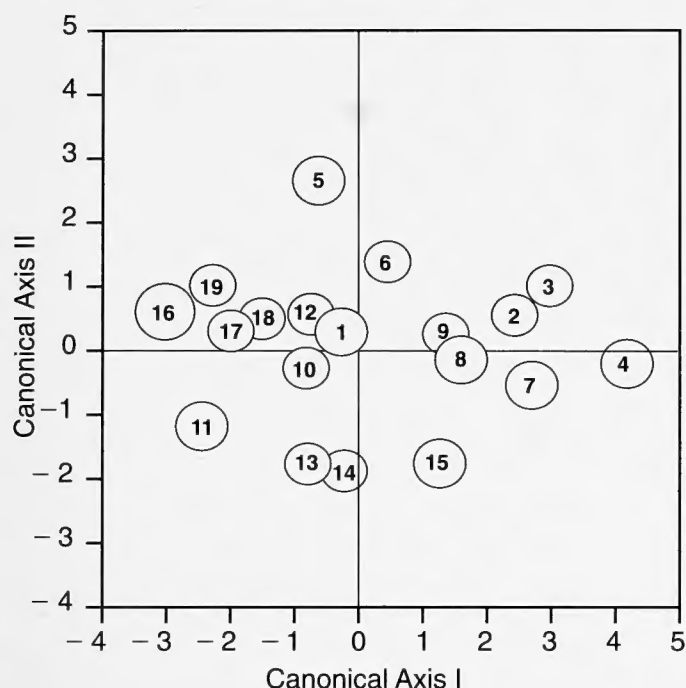


Fig. 5. Plot of mean canonical discriminant scores for 19 samples of *Bufo valliceps*. Circles represent approximate 95% confidence intervals around each mean score. For purposes of clarity, prediction intervals are not shown, but these have a diameter of 2.45 units on each axis and, therefore, would indicate substantial overlap among many groups. Sample sizes for each population are shown in Table 4.

granular dorsal skin texture, granular ventral skin, relatively small, ovoid or subtriangular parotoid glands, an indistinct lateral descending row of tubercles, and a relatively wide, distinct, middorsal pale stripe (Fig. 6). The dorsal pattern lateral to the middorsal stripe may be strongly marbled, with either dark brown or tan-yellow shades predominating, mostly pallid, or nearly uniform dull brown; usually, there is a distinct dorsolateral pale area, along the dorsal border of the lateral descending row of tubercles. The venter is always immaculate and may appear (in preservative) pale yellow, whitish, or dull tan. The lateral descending row of tubercles is bordered ventrally by a dark brown stripe that becomes thin or broken on the flanks.

The tubercles on all dorsal surfaces of the body are large, densely distributed, sharply pointed, and keratinized. Usually, there is a single keratinized apex surrounded by a granular patch of keratin and often these are coalesced into a keratinous blotch from which a pointed center arises. These tubercles give the toad a rough, granular texture. The ventral skin texture is granular with many tiny, pointed tubercles, each bearing a single keratinized apex. Males and females also have heavy layers of keratin on the peripheral surfaces of all cranial and facial crests. The parotoid glands may be relatively large and ovoid, as in individuals from the Grijalva Valley, in Chiapas and adjacent areas of Huehuetenango, Guatemala (discussed

Table 3. Standardized (pooled within-group variances) coefficients for the canonical variables on the first two canonical axes; cumulative proportion of dispersion (variance) displayed on each axis shown in parentheses.

Variable	Canonical Axis I (0.987)	Canonical Axis II (0.995)
SVL	-0.79626	0.65282
FML	0.29343	-0.01370
ML	0.36157	0.04695
RUL	0.36908	-0.29779
HDL	0.04474	-0.25055
FT	-0.85926	0.80126
HL	0.40648	1.13339
HW	-0.61490	-1.64387
ORB	0.72146	-0.20203
END	0.61903	-0.22798
TYMP	0.20178	0.30574
SPTYMP	-0.33749	0.31473
PARL	0.34510	0.20732
PARW	-0.48930	-0.76280

below under *B. valliceps wilsoni*), or relatively small and distinctly triangular, as in some individuals from the Yucatan Peninsula. Most individuals, regardless of origin, have ovoid or subtriangular parotoid glands.

The color patterns among *Bufo valliceps* from southern Mexico and Central America are extraordinarily variable, even among individuals from a single locality. In some, the dorsal pattern is uniformly dark brown, or nearly so, with or without a thin, middorsal pale stripe, whereas in others, it is nearly uniformly tan and lacks dorsal markings. Other individuals are pale brown with distinct black or dark brown, paired markings, with or without a distinct interorbital bar, or pale brown with a complex marbled pattern of small dark brown blotches. Nearly every intermediate pattern and combination of the above extremes may be found among *B. valliceps* from Veracruz to Nicaragua. Laterally, all individuals have a dark area below the lateral descending row of tubercles. This dark area is wide, dark brown or pale gray, and extends from the tympanic area, or the level of the insertion of the arm, onto the flank; in some individuals, the dark area becomes diffuse and disappears anterior to the flank. The ventral pattern usually is dull cream with any number of diffuse or distinct dark markings that sometimes are expressed as a uniform dull gray area on the throat and pectoral area; few individuals have immaculate venters.

Southern toads have a smoother skin texture than do those from the northern areas. The tubercles on the dorsum of the body of southern toads are less numerous, low, round and bear a small patch of granular keratin; few individual tubercles are pointed, and some specimens have little keratin atop the dorsal tubercles. The ventral skin texture is smoother than in the northern toads, with many low, round tubercles; some southern individuals have

Table 4. Jackknifed classification matrix from the 14-variable model generated by the stepwise DFA of 19 sample populations of *Bufo valliceps*. The bold figures indicate the number of specimens correctly classified; the number in parentheses indicates the number of specimens in that sample.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
1	7 (8)	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
2	0	2 (15)	2	2	2	0	4	2	0	0	0	1	0	0	0	0	0	0	0
3	0	2	5 (14)	4	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0
4	0	0	2	8 (13)	0	0	2	0	0	0	0	0	0	0	1	0	0	0	0
5	0	0	0	0	11 (12)	1	0	0	0	0	0	0	0	0	0	0	0	0	0
6	2	2	1	0	0	9 (18)	0	0	0	0	0	2	0	0	0	0	1	1	0
7	0	2	1	2	0	0	2 (8)	0	0	0	0	0	0	0	1	0	0	0	0
8	0	1	0	2	0	0	1	2 (8)	1	0	0	0	0	0	0	0	0	0	0
9	0	1	0	0	0	0	0	1	11 (19)	2	0	2	1	0	0	0	0	0	0
10	0	0	0	0	0	0	0	1	1	6 (15)	2	1	1	0	0	2	0	0	1
11	0	0	0	0	0	0	0	0	0	0	12 (13)	0	0	0	0	1	0	0	0
12	1	0	0	0	0	0	0	0	1	0	0	23 (28)	2	0	0	0	0	0	1
13	1	0	0	0	0	0	0	0	0	0	0	2	11 (19)	2	2	0	1	1	0
14	0	1	0	0	0	0	2	0	0	0	1	0	1	14 (19)	1	0	0	0	0
15	0	0	0	0	0	0	0	0	0	1	0	0	0	3	6 (12)	0	0	0	0
16	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	7 (11)	1	1	0
17	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	4	1 (22)	1	0
18	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	1	9	9 (15)	2
19	0	0	0	0	1	0	0	0	0	0	0	0	2	0	0	2	1	1	6 (14)

pointed and unkeratinized tubercles on the venter and, therefore, have a relatively granular ventral texture similar to that of the northern toads. The tubercles forming the lateral descending row may be indistinct or distinct, and low and round, or high and pointed. Few adults of either sex have keratin overlying the peripheral margins of the cranial crests; when present, the keratin is thin and brown, rather than black.

Northern and southern *Bufo valliceps* differ in overall size, color pattern, and skin texture. However, I have not identified a clear disjunction in the distribution that corresponds with these characteristic differences. Samples from northern Veracruz and southern Tamaulipas are intermediate in size (Figs. 2, 3; Sample 9) and have a mixture of color patterns and skin textures (among and within individuals) typical of both more northern and southern samples.

DISCUSSION

It is clear that there is considerable morphological variation in *B. valliceps* across its extensive range, and that there are few apparent trends that correspond with geographical parameters. These toads vary extremely in size, color pattern, parotoid gland shape, and skin texture. The inconsistent variation has caused many specimens to be misidentified and resulted in general taxonomic confusion with respect to several populations of crested toads in Mexico and Central America (Mendelson, 1994, 1997 a,b, 1998). The range of *B. valliceps*, as considered here (Fig. 1), includes both Central America and a substantial area of North America. Across this range, and indeed east-to-west from Louisiana to western Texas, populations of *B. valliceps* are subject to diverse environmental regimes of seasonal rainfall and freezing temperatures. Moreover, this toad occurs from sea level to at least 1700 m, and these populations are subject to different local conditions of rainfall and cloud cover. Few clear morphological trends seem to be associated with these environmental variables.

BODY SIZE AND ARIDITY

Lee (1993) reviewed the theoretical literature that predicts that amphibians, because of their high rates of cutaneous evaporative water loss, presumably *should* adapt to arid environments by evolving larger body size in order to achieve a favorable surface-to-volume ratio. He also pointed out that no rigorous test of this prediction had been carried out prior to his work with the ubiquitous tropical treefrog *Smilisca baudinii*. Lee (1993) compared morphometric variables among samples of *S. baudinii* along a sharp precipitation gradient that exists on the Yucatan Peninsula. He found, contrary to the theoretical predictions, that there was no direct correlation between body size and aridity in this species and that, in fact, frogs from the more mesic base of the peninsula were larger than those from the more arid coastal tip. However, Lee (1993) did find that frogs from the drier, more seasonal areas have slightly smaller appendages—a finding consistent with the surface-volume desiccation argument. My analysis of overall size among

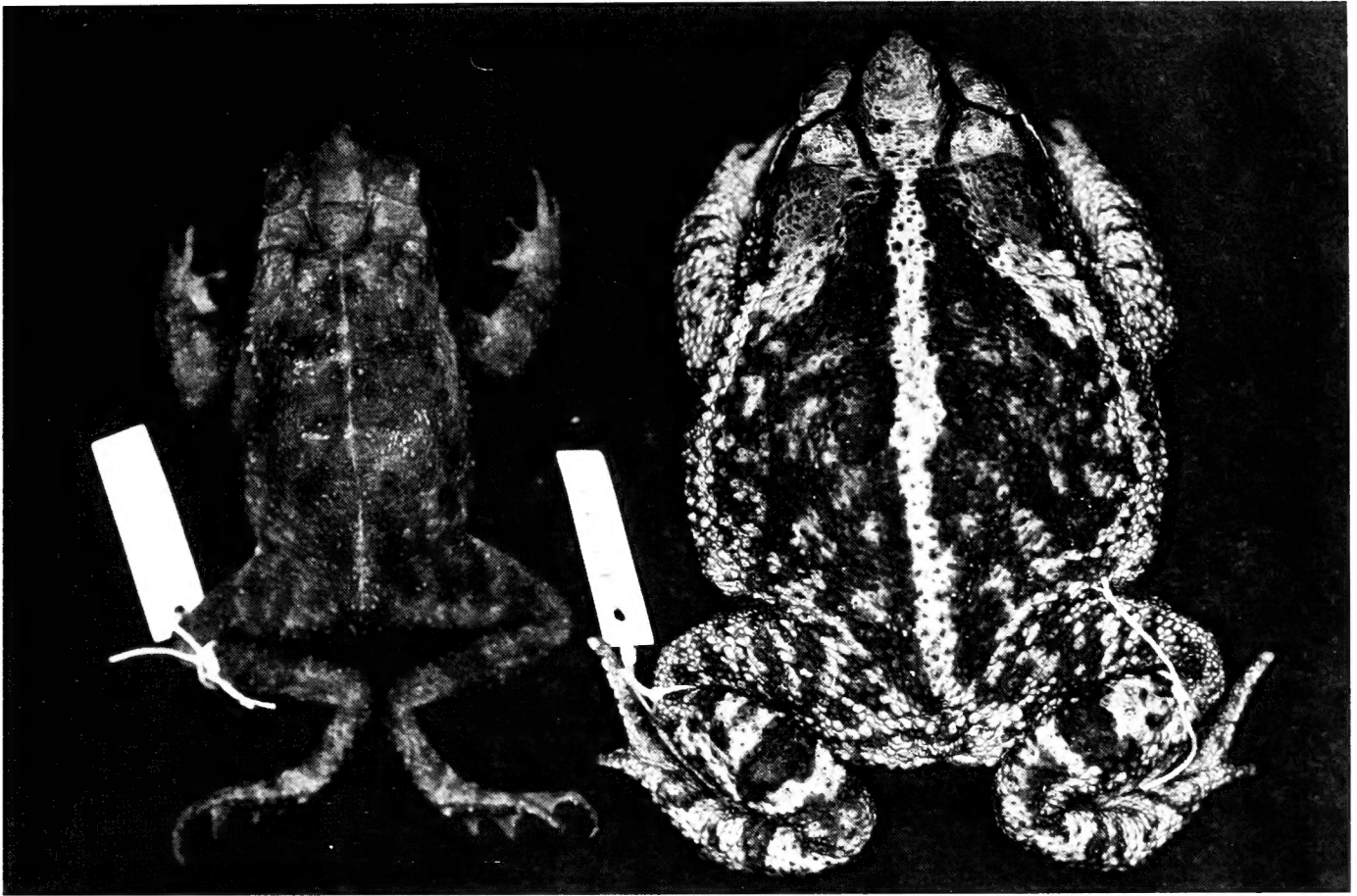


Fig. 6. Comparison of typical adult males from Alta Verapaz, Guatemala (left; KU 65551; SVL = 60.8 mm) and Coahuila, Mexico (right; KU 47011; SVL = 86.3 mm). Note differences in overall size and the distinctive middorsal stripe of the male from Coahuila.

samples of *B. valliceps* across the same precipitation gradient on the Yucatan Peninsula revealed that although there are differences in overall size among populations of *B. valliceps* in this area, these differences do not seem to be correlated with the precipitation gradient. Similarly, among samples from throughout the range of *B. valliceps*, there is considerable variation in overall size, and the largest toads were from relatively arid areas in Texas, Coahuila, and Nuevo Leon. However, toads from other arid areas, such as the Grijalva Valley in Chiapas, were quite small. Conversely, although the smallest toads did come from relatively wet areas, not all samples from wet areas were particularly small.

Lee (1993) discussed the inherent difficulty in adequately testing a seemingly simple hypothesis such as correlation between body size and aridity. The elegance of his study lies in the fact that he identified the Yucatan Peninsula as a perfect testing ground for such a study; it is a relatively small area and is nearly uniform with respect to elevation and temperature profile. The environments from which my samples across Middle America originated differ substantially in nearly every environmental aspect—

not the least of which includes relatively severe winters (with snowfall) at the northern periphery of the range. These climates are so different that I deem them incomparable. The great amount of morphological variation in *B. valliceps*, and the lack of obvious trends with respect to geography and climate, lead me to concur with Lee (1993) that simple predictions of correlation between morphology and climate are easier to generate than to demonstrate; such correlations do not seem to pertain to *Bufo valliceps*.

CREST HEIGHT AND ELEVATION

A series of papers (Porter, 1963, 1964; Blair, 1966, 1972; Branson, 1995) reported that there is a direct correlation between the height of the cranial crests and elevation, and they used the population near Cuautlapam, Veracruz (near 1000 m in the Sierra Madre Oriental) as an example. These claims, presented without supporting data, seem to have their only basis in a figure presented in Porter's (1962; fig. 26) dissertation. Because the original data used to support this apparent correlation are not widely available, and because such a correlation between morphology and elevation would be interesting, if true, I review Porter's (1962) treatment of the matter.

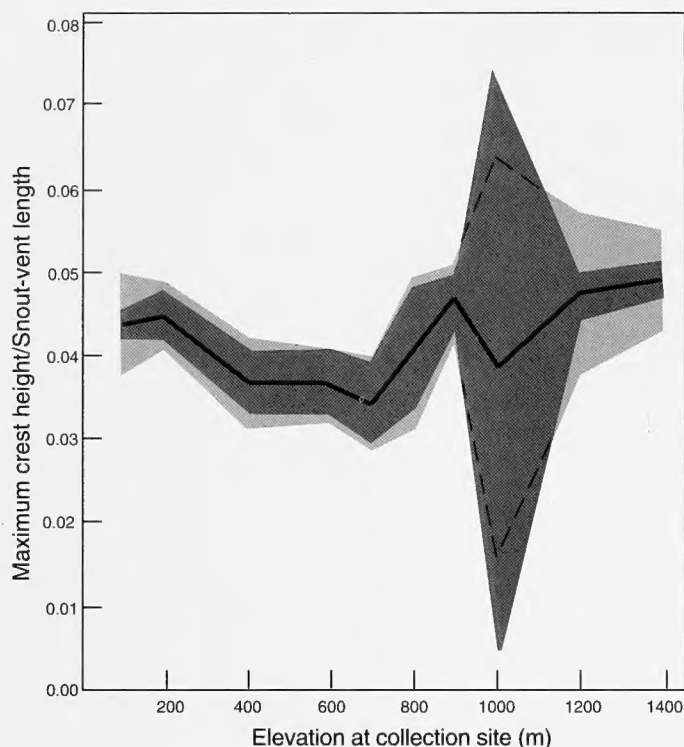


Fig. 7. A precise representation of Porter's (1962) Figure 26 showing the relationship between crest height and elevation at collection site. Porter's original caption: "The relationship between maximum crest height and the elevation of the collecting site for *B. valliceps*. The black line indicates the mean cranial crest height, the [light] gray area one standard deviation either side of the mean, the [dark gray] area two standard errors either side of the mean. All collecting site elevations were rounded off to the nearest 100 meters."

Porter's original figure (1962; fig. 26) is represented in Fig. 7; several points require attention. First, Porter's concept of *Bufo valliceps* included all specimens referable to *B. macrocristatus* (Mendelson, 1997a); this is a sexually dimorphic, montane species in which females have dramatically enlarged crests. Other specimens that Porter referred to *B. valliceps* subsequently have been referred to other species such as *Bufo spiculatus*, which have larger cranial crests than *B. valliceps* (Mendelson, 1997b). Because Porter did not provide a list of the specimens included in his analysis, it is impossible to determine which, if any, of these other crested toads were mixed in with his samples of *B. valliceps*. Second, Porter apparently did not separate the sexes for his morphometric summaries; this is particularly unsettling because females are larger than males in overall size and may differ somewhat in certain proportions, especially in the case of specimens now referred to *B. macrocristatus*. Third, Porter (1962:5) did not describe adequately how he measured crest height; I abandoned my own attempts to measure this feature because I could not develop a repeatable measurement based on homologous landmarks. In summary, Porter's analysis of correlation between crest height and elevation is suspect because it seems likely that he included among his samples individuals referable to

other species, including upland species with greatly enlarged crests; moreover, he did not account for sexual dimorphism in size, and he did not describe adequately his measurement techniques.

Pursuant to my concerns with Porter's methodology, it is interesting to note that, despite how the results have been presented in subsequent literature, there seems to be no actual direct correlation between crest height and elevation (Fig. 7). Comparison of the mean crest height/SVL ratios from below 200 m and near 1400 m indicates less than 1% difference, and the slope of the line between these two points probably does not differ significantly from zero; Porter did not perform a regression analysis on these data. What is evident from this plot is a remarkable amount of variation in specimens from an elevation of about 1000 m; most specimens of *B. macrocristatus* have been collected from near 1000 m of elevation (Mendelson, 1997b).

TAXONOMIC ISSUES

In a series of papers (Mendelson, 1994; 1997a,b,1998), I have resolved much of the taxonomic confusion surrounding populations of crested toads that previously (and inconsistently) were referred to *B. cavifrons*, *B. cristatus*, and *B. valliceps*. I removed the taxon *B. valliceps macrocristatus* Firschein and Smith from the synonymy of *B. valliceps*, recognizing it as a full species, and transferred the taxon *B. valliceps microtis* Werner to the synonymy of *Bufo coccifer*. Two taxa remain to be considered—*B. valliceps wilsoni* Baylor and Stuart and *Bufo nebulifer* Girard.

Baylor and Stuart (1961) described the subspecies *B. valliceps wilsoni* based on a series of specimens collected by L. C. Stuart at Jacaltenango, Huehuetenango, Guatemala. This locality is in the upper Grijalva Valley, at the base of the Sierra de los Cuchumatanes. The region is quite dry and thorn scrub forest prevails. The key diagnostic features of this taxon are the presence of relatively large parotoid glands and short supratympanic crests. The authors were careful to compare their specimens with *B. valliceps* from many other areas, and chose a comparative specimen from El Petén, Guatemala to illustrate the distinctive nature of *B. valliceps wilsoni* (Baylor and Stuart, 1961:figs. 1, 2); they also cautiously pointed out that recognition of this new taxon was not meant to imply that all other populations referred to *B. valliceps* were conspecific. Their choice of a comparative specimen from El Petén exaggerates the distinctness of *B. valliceps wilsoni*, because some specimens from the base of the Yucatan Peninsula have unusually small and triangular parotoid glands, as does the specimen in their figure. When specimens from the Grijalva Valley are compared with specimens from other areas of Mexico, the differences in the size and shape of the parotoid glands and the length of the supratympanic crests are less apparent. Nonetheless, L. C. Stuart's careful eye, particularly with respect to the stout nature of the supratympanic crests, prevails in this case. Individuals from the Grijalva Valley are consistently different from *B. valliceps* from other areas. However, I do not recommend recognition of the taxon *B. wilsoni* at this time.

Baird and Girard (1852) described *Bufo granulosus* based on a specimen collected "between Indianola and San Antonio," Texas, during the U.S.-Mexico boundary survey. Inasmuch as this name was preoccupied by *Bufo granulosus* Spix 1824, the replacement name *Bufo nebulifer* Girard 1854 was proposed. Peters (1863) placed *B. nebulifer* in the synonymy of *B. valliceps* Wiegmann 1833. The north-

ern *B. valliceps* are larger and have a distinctive pattern and skin texture compared to *B. valliceps* from Central America; these differences perhaps warrant recognition of *B. nebulifer*. However, in light of the general variation in these continuous characters among and within populations of *B. valliceps*, and the lack of a discrete character by which to diagnose the northern and southern populations, I do not propose recognition of *B. nebulifer* at this time.

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APPENDIX

SPECIMENS OF *BUFO VALLICEPS* EXAMINED

GUATEMALA: ALTA VERAPAZ: 16.4 km W Tucurú (UTA A-7418-19, 7421-28); Finca Los Alpes (KU 65551). CHIQUIMULA: Esquipulas (UMMZ 106794). EL PETÉN: 8 km NNW Chinajá (KU 55873-74, 58376, 55878-81); 10 km NNW Chinajá (KU 55887); 11 km NNW Chinajá (KU 55891-92, 55894-96); 16 km NNW Chinajá, Río San Roman (KU 55900, 55911-12, 55913-16); 15 km NNW Chinajá (KU 55918); 8.6 mi W El Cruce (KU 156414-15); 1.9 mi S La Libertad (KU 156409-13); ca 4 mi N Poptun (KU 156396-403); 3 mi S Tikal (156416-20); Tikal (LSUMZ 28138-39); Toocog, 15 km S La Libertad (KU 55920); Uaxactun (KU 156390-95). HUEHUETENANGO: Cuilco, Carretera Cuilco-Canibal, 1105 m (UTA A-47564); Jacaltenango (UMMZ 119371-74, 119380, 126298). IZABAL: Quirigua, Puebla Ranch, United Fruit Company (CAS 70828-35, 70837-38); 1.8 km SW Morales turnoff on Hwy CA-9, 85 m (KU 190101); 4 km ENE Morales turnoff on Hwy CA-9, 85 m (KU 190102); Río Blanco, 120 m (KU 190098), 99; 3.2 km SW Puerto Santo Tomás, 12 m (KU 190132); Aldea

Vista Hermosa, Los Amates, 700 m (KU 190141-42); Aldea Vista Hermosa, Los Amates, 135 m (KU 190146-47); El Estor, Club Sechoc (UTA A-34048); Puerto Libre Hotel, at road fork between Puerto Santo Tomás and Puerto Barrios (UTA A-21677-78); N slope Sierra de las Minas, Finca Pueblo Viejo (UTA A-28869-71, 28874, 28876, 28878-79, 28885, 28894, 28898); Nickel Mine Airstrip at El Estor (KU 7429); 1.7 mi W El Estor, Las Dantas (UTA A-7430-31); Montañas del Mico, 1.4 km WSW Puerto Santo Tomás, near Las Escobas (UTA A-24738-39); Sierra de Santa Cruz, 10.0 km W Finca Semuc headquarters, Semucoch (UTA A-24932-33, 24942); Montañas del Mico, 5.1 rd km WSW Puerto Santo Tomás, Las Escobas (UTA A-33046). ESCUINTLA: circa 26 air km SE Escuintla, Finca El Caobanal, 100m (UTA A-28957-58, 28961); 7.7 km SSW Santa Lucía Cotzumalguapa, on road to Las Playas (UTA A-29009-20); [Finca] El Salto, near water tank by the falls (MVZ 88352); Finca El Salto, ca 2 km E Escuintla, 1000 ft [304 m] (MVZ 104375); Río Guacalate, near Masagua (USNM 125240-45). JALAPA:

6.9 km SE Jalapa on Rn 19 (TNHC 31345, 31500-08). JUTIAPA: Finca La Trinidad, near Casa Grande (UMMZ 107818). RETALHULEU: Hacienda Casa Blanca, 1-3 km N and NW Casa Grande (UMMZ 107820); 3.2 km N Champerico (UTA A-25849-64). SACATEPEQUEZ: 1.4 km SSE San Antonio (TNHC 31492-96). SAN MARCOS: road between La Blanca and Tilapa, 3 m (UTA A-47538). SANTA ROSA: [11.9 km] W Chiquimulilla, 49 m (KU 97704-12). SUCHITEPEQUEZ: Mazatenango, Finca El Horizonte (LSU 9323, 9328); Río Nahualate, 9 mi NNW Tiquasate (Depto. Escuintla) (USNM 125307).

HONDURAS: ATLÁNTIDA: Corozal, ca. 15 km E La Ceiba (LSUMZ 21611, 21614). CHOLUTEC: 28.8 mi S Sabana Grande (LSUMZ 33625). COLÓN: Puerto Casilla (LSUMZ 22473); Río Grande (LSUMZ 33626); Trujillo (LSUMZ 22491, 27743). COPAN: 4.3 mi SW Santa Rosa de Copan (LSUMZ 22457); 9 km S La Entrada (LSUMZ 22588-89, 22591-92, 22597). CORTES: W of San Pedro, Hacienda Santa Ana (FMNH 4617-20, 4624, 4626, 4629-30); 12 km E San Pedro, Lake Ticamaya (FMNH 4632); Copan (FMNH 28513); 3.2 km NE San Pedro Sula (KU 97713-22); Cerro Cusuco, 1520 m (KU 209270); Quebrada de Colorado, ca Buenos Aires (KU 194223). GRACIAS A DIOS: Tancin, 15 km NW Puerto Lempira (LSUMZ 21600). OLANCHO: 0.5 km WNW Catamacas (LSUMZ 21590, 21592-94); Escuela Nacional de Agricultura, 4.5 km SE Catamacas (LSUMZ 21597); 3.4 km N San Esteban, 510 m (KU 209271); 15.7 km S San Esteban, 480 m (KU 209272); 5.6 km S San Esteban, 450 m (KU 209273); 4.6 km S San Esteban, 440 m (KU 209274-75). SANTA BARBARA: W side Lago de Yojoa, 775 m (KU 65544); San Jose de los Andes, 1610 m (KU 209279-80). YORO: 2 km S Coyoles on Río Aguan, 120 m (KU 101179); Rancho San Lorenzo, 25 km WSW Coyoles (LSUMZ 21606); 0.5 km N Coyoles (LSUMZ 21607); Santa Rita (KU 192295); Subirana Valley (FMNH 21789-21792).

MEXICO: CAMPECHE: 5 km S Champotón (KU 70991-71003); 3 km N Hopelchen (KU 75231-33); Dzibalchen (KU 75234-37); 7.5 km W Escárcega (KU 71004-71021); 1 km W Escárcega (KU 71022-33). CHIAPAS: 26 km N Ocozocoautla (UTEP 5817-19, 5823); 1 km N Ocozocoautla (UTEP 5821, 5824, 5831); 20 km N Ocozocoautla (UTEP 5822); 23-24 km N Ocozocoautla (UTEP 5825-27); 2.4-5.3 km W Ciudad Cauhuatemoc (KU 97723-26); 1 km N Tuxtla Gutierrez (UTEP 5828-29, 5833); 54.5 km S Pueblo Nuevo Solistahuacan (TNHC 27046, 27048, 27052); San Fernando (TNHC 25233-34, 25237, 25239-40); 38 mi W Cintalapa (TNHC 27057-59); 3 mi E Cintalapa (TNHC 27054-55, 27358); 10 mi E Cintalapa (TNHC 27359). COAHUILA: spillway canal below Don Martin dam (KU 128778-86); 2-6 mi W Sacramento (KU 47010-13); Río Salado de los Nadadores, El Cariño

(KU 80310-15). HIDALGO: 12.5-38.5 km SW Huejutla (UTAA-13110, 13113-19, 13121-31). NUEVO LEÓN: La Huasteca Canon (KU 192507-19). OAXACA: 6 km N Palomares (KU 58333-60). QUINTANA ROO: Pueblo Nuevo X-Cán, 10 m (KU 71036-50). VERACRUZ: 12.8 km N Acayucan (KU 97672-85); Cuautlapan (KU 97686, 105521-26); 16 km NE Fortín de las Flores (KU 97687-96); Portero Viejo (KU 25836-45, 25847-51, 26720-24); Cuautlapan (TNHC 27014-19, 17, 27123-28). YUCATÁN: Chichen Itzá (KU 71059-61); FMNH 26956-58); 12 km E Chichen Itzá (KU 71062); 17 km N Piste on rd to Tzitsin (KU 751950); Xocchel (KU 156435-37); 12.3-16.8 mi E Izamal (KU 156439-41); Mérida (FMNH 40653-58, TNHC 33224).

NICARAGUA: ESTELÍ: 7 km N, 16 km E Condega, 1200 m, (KU 85253-57); 5 km N, 14 km E Condega, 40 m (KU 85251). MATAGALPA: 10.5 km N, 9 km E Matagalpa, 960 m (KU 85258-62). NUEVO SEGOVIA: 5 km N, 2.5 km E Jalapa, 680 m (KU 112722-26); 1.5 km N, 1 km E Jalapa, 660 m (KU 112727-39). ZELAYA: Bonanza (KU 85263-67, 101178); El Recreo, S side Río Mico, 25 m (KU 112708-21); 11 mi W Muelle de los Bueyes, Hwy 7 (KU 136410).

USA: LOUISIANA: EAST BATON ROUGE PAR.: 4 mi S Baton Rouge (KU 22519-26; 22527) 1.6 mi E jct River Road and Brightside Dr. (KU 145509); ca 2 mi S LSU campus on River Road (KU 145510); 0.9 mi S East Feliciana (KU 145511-16). LIVINGSTON PAR.: ca. jct rtes 16 and 1026 (KU 145507). SR. CHARLES PAR.: 3.6 mi N Norco (KU 145508). TEXAS: ATASCOSA CO.: Benton (KU 11997). BEXAR CO.: Somerset (KU 20045-46); Helotes (KU 11590). BRAZORIA CO.: 5 mi E Liverpool (KU 44884-908); 1 mi S Freeport (KU 44909-15). CAMERON CO.: Brownsville (KU 11591-608, 14100-01, 14309-32). DALLAS CO.: Dallas (KU 33556); South Cockrell Hill Road (UTA A-581-83); Oak Cliff (UTA A-1861). PARKER CO.: 2.0 mi NW Wheatland (UTA A-7228). STARR CO.: Río Grande (KU 11998-99). TARRANT CO.: 8.0 mi W Fort Worth (UTA A-486); Arlington (UTA A-384, 9144, 17450-52, 41964); Benbrook-Aledo Road (UTA A-1223); E of US Hwy 377, jct of Mary's Creek and Vickery Blvd (UTA A-7390). UVALDE CO.: FM 1022, 2.6 mi S Rte 90 (UTA A-37382). TRAVIS CO.: Austin (TNHC 15643-47, 15649-53, 15654-57). VAL VERDE CO.: Moose Canyon at jct Pecos River (KU 195052); Route 90, 1.4 mi E loop 25 (UTA A-37378-37380); State Hwy 163, 67.6 km S jct Interstate Hwy 10 (UTA A-17453); 18 mi NE Comstock (TNHC 32355-57). WALKER CO.: Park Road 40 at entrance Huntsville State Park (UTA A-37279-80); 0.25 mi down Fish Hatchery Rd (UTA A-41586); New Waverly (UTA A-40957); Texas Dept. of Corrections, Ellis Unit (UTA A-41696-98); Pritchett Field (UTA A-42327-48). WEBB CO.: 4 mi N Laredo (KU 23383).